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Notes on the Biology of Some Trinidad Swifts[1]

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(Text-figure 1)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest preserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe, Zoologica, 1952, 37 (13): 157-184.]

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THE biology of the neotropical swifts is not well known. For the genera *Chaetura* and *Cypseloides*, with which this paper is concerned, only Beebe (1949), Haverschmidt (1958) and Sick (especially 1948, 1951, 1958, 1959) appear to have made significant recent contributions. They are difficult birds to watch and many are difficult to identify in the field. Several species have never been found nesting.

Compared with the mainland of South America, where, to judge from published data, it is unusual for several species to be common in the same area, Trinidad is especially suitable for field studies of swifts. Here, on an island measuring some 50 by 30 miles, seven species are resident: five of them are known to breed and all seven probably do so. Only one species can be called rare. Probably nowhere else in the neotropical region can so many breeding species of swifts be found in so small an area.

During 4½ years' residence in Trinidad, I made such observations on the swifts as opportunity permitted. They were not a main subject of study, but their abundance brought them constantly to notice. Nests of two species were found in sufficient numbers for a limited analysis of breeding season, number of broods, nesting success and other aspects of breeding biology. In addition, five species were caught in mist-nets, two of them in good numbers, and a sixth was twice caught by hand. This paper presents the information thus collected.

I have followed Lack (1956) in his wide definition of the genus *Cypseloides*. For vernacular names, I have followed Eisenmann (1955) except that I have preferred to use the more evocative name Cloud Swift for *Cypseloides (Streptoprocne) zonaris*.

I am grateful to my wife for much help with the field work, to Dr. Wilbur G. Downs for photographic assistance, and to Charles T. Collins, J. Dunston and R. P. ffrench for visiting nests at times when I was unable to do so. C. T. Collins discovered one of the Chestnut-collared Swift nests and J. Dunston three of the Short-tailed Swift nests. This study, part of a wider program of field studies on the biology of neotropical birds, has been generously supported by National Science Foundation grants G 4385 and G 21007.

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Distribution, Status and Feeding Habits

The Chaetura Species

The Short-tailed Swift (*C. brachyura*), Band-rumped Swift (*C. spinicauda*) and Gray-rumped Swift (*C. cinereiventris*) are all common species, but they have different local distributions. The Short-tailed Swift is the most widespread, occurring all over the island; it is the only species regularly occurring over open country and towns. It may be seen throughout the Northern Range (the range of forested mountains, up to 3,000 feet high, running along the north side of Trinidad), but is less common there than the other two species. The Band-rumped Swift occurs generally over forested country and wooded savanna, in both lowlands and hills. The Gray-rumped Swift is common in the Northern Range; I did not see it elsewhere.

The fourth species, Chapman's Swift (*C. chapmani*), is very little known. Apart from the original series collected by Chapman in 1894, only a few specimens have been collected, in widely scattered localities from Panama to central Brazil (Wetmore, 1957). I several times thought that I saw Chapman's Swift among mixed parties of swifts in the Northern Range, but the first positive evidence was obtained on November 27, 1960, when one was caught in a mist-net at 1,800 feet at the head of the Arima Valley in the center of the Northern Range. Having had the opportunity to examine a living bird in the hand and to note its field characters as it flew away on release, I later was confident that I saw Chapman's Swift on two occasions, once in the same place and once in the lower part of the Arima Valley. But hundreds of the three other *Chaetura* species were examined before these were seen. From these few records, and from Chapman's specimens collected at Valencia at the foot of the Northern Range about six miles east of the Arima Valley, we may conclude that Chapman's Swift is probably resident in the Northern Range in small numbers.

I obtained no evidence for any differences in feeding habits of the three common *Chaetura* species in places where they occurred together, though quantitative observations might eventually show fine differences. All feed regularly from ground level to several hundred feet up. They commonly skim close to the ground in sheltered clearings in the hills, probably because of the abundance of flying insects in such places, and when termites swarm after wet weather they all come low to feed on them. In wet weather great flocks of them move rapidly up and down the valleys and across the watersheds, avoiding the rain-storms.

The Cypseloides Species

Chestnut-collared Swifts (*C. rutilus*) are common in the Northern Range, but they feed much higher than the *Chaetura* species, and presenting only a black silhouette are often less easy to identify with certainty. Because they fly high, they were the only species resident in the Arima Valley never to be caught in a mist-net. They are usually seen in ones or twos, or small parties. Only once were many seen together; on September 3, 1958, large numbers were seen flying around the summit of El Tucuche (3,068 ft.), the second highest peak in Trinidad, and with them only a very small number of four other species. This was a post-breeding aggregation; many were seen to be moulting their wing-feathers.

The Cloud Swift (*C. zonaris*), the largest and most majestic of the New World swifts, is a migrant to Trinidad. The first birds arrive in July (first dates: 1957, end of July; 1958, July 27; 1959, July 14; 1960, mid-July; 1961, July 8). August and September are the months when the greatest numbers are present. By October their numbers have begun to decline, but a few are seen irregularly until February. This probably represents a post-breeding dispersal from breeding areas in the Andes of Venezuela to the west of Trinidad. A number of specimens collected by Roberts (1934) on August 28 were all completing their moult. I obtained three specimens, in late July and early August; all appeared to be juveniles and were not moulting.

Cloud Swifts are erratic in their appearance, being present in great numbers one day and absent the next. They feed at all heights, and range rapidly and widely over the island. It is likely that at least on occasions they spend the night in the air, as the European swift *Apus apus* has been found to do. On August 11, 1957, I watched a large flock at dusk in the Arima Valley, in the center of the Northern Range. They were spiralling upwards, gradually drifting out of sight behind some hills. Some at least were still circling when poor light prevented further observation. Cloud Swifts roost on cliffs, in clefts and behind waterfalls (Sutton, 1951). There are few suitable cliffs in Trinidad, except the sea cliffs of the north coast, and it seemed unlikely that the large flock I was watching could all have found roosting places for that night.

Belcher & Smooker (1936), on rather unsatisfactory evidence, record another migrant swift for Trinidad, the Black Swift (*C. (Nephoecetes) niger*). This species would be expected to occur occasionally on passage, and further observation may confirm that it does so.

Other Species

Panyptila cayennensis is widespread in small numbers, breeding from near sea level to at least 1,000 feet in the Northern Range. My records of its nests are all in the northern and eastern parts of Trinidad, but the other parts of the island were visited much less often. *Panyptila* feeds high above the ground and is usually only to be identified with binoculars.

Reinarda squamata is confined to savanna and swamp forest in the east of Trinidad, following the distribution of the palm *Mauritia setigera,* on which it nests. It commonly feeds close to the ground.

The Breeding of *Chaetura brachyura*

Nest-site

Belcher & Smooker give the only previous records of the nesting of the Short-tailed Swift in Trinidad. They reported one nest in a chimney, with 3 eggs on June 20, and one nest in a sea cave, with 3 eggs on June 3. There are no breeding records from elsewhere, but observations by Bond (1928, and *in litt.*) suggest that Short-tailed Swifts nest in chimneys in St. Vincent.

I discovered a small breeding colony of Short-tailed Swifts by chance on May 7, 1957, when, watching swifts flying low over bushy savanna near Valencia, I saw a bird suddenly drop out of sight in the grass. I found that it had entered a concrete man-hole, part of an abandoned drainage system constructed during the war when this savanna was the site of a U.S. Air Force camp. A search made in the immediate area revealed eight other man-holes which swifts could enter, and three more were eventually found on other parts of the savanna. These holes were kept under regular observation until September, 1961, giving complete records for five breeding seasons.

Some other breeding sites were found. Short-tailed Swifts were seen during the breeding season entering and leaving sea caves in the rocky north coast of Trinidad, and in Huevos Island off the northwest corner of Trinidad, but no accessible nests were found. One pair was found nesting in a chimney in Arima. Finally, a pair nested for two seasons in a nest-box which I erected 30 feet up against the trunk of a large Chataigne tree (*Pachira insignis*), 500 feet above sea level in the Arima Valley.

The use of this nest-box was unexpected, as all previous records of their nests had been in caves, man-holes or chimneys, and the species is less characteristic of forest than the other *Chaetura* species. The history of its occupation was as follows. On July 9, 1959, a pair of Band-rumped Swifts had been observed entering a natural cavity some 30 feet up in the trunk of this tree, and from observations made on July 11 it was clear that they were feeding young. A ladder was put up to the hole, but the nest could not be seen. The entrance was narrow, and the hole was irregular and descended several feet. Since Band-rumped Swifts had never been found nesting, I subsequently blocked up the natural hole and fixed a nest-box near by, 5 feet long and 1½ feet square in section, with a slit-shaped hole near the top about 5 inches wide (about one inch wider than the tree-hole). Occupation of the box was first noted on June 22, 1960, when a pair of Short-tailed Swifts were found to be feeding five half-grown young. In 1961 a pair of Short-tailed Swifts again nested in the box. In both years a pair of Band-rumped Swifts, presumed to be the former owners of the tree-hole, were several times seen about the tree. It seems that, in making the hole of the box a little wider than the tree-hole, I inadvertently made it big enough for Short-tailed Swifts to enter and they were thus able to dispossess the smaller Band-rumped Swifts (the mean wing-length of the two species differs by about 17 mm.). It is probably because of their larger size that Short-tailed Swifts normally nest in caves and man-made cavities, while the smaller *Chaetura* species, as far as known, nest in tree-holes.

It was of interest that when the Short-tailed Swifts left the box after feeding the young, they used to fly off down the valley in the direction of the savanna three miles away. They would return from the same direction.

Breeding Season

When I first found the nesting colony in the man-holes in early May, 1957, nests were being built and none had eggs until a week later. Table I shows the monthly distribution of the 86 nestings recorded at this colony in the five years. Breeding begins in April or early May and continues until August or early September (the three breeding dates obtained at other sites, and Belcher & Smooker's two records, all fall near the middle of this period). Numbers were too few to reveal slight annual variations, but there were no marked differences in breeding season in the five years.

There was usually a regular succession of nestings in each hole in the course of the breeding season, either in the same nest or, less often, in a succession of nests. No hole ever contained more than one occupied nest at the same time. The intervals between the nestings suggested, as would be expected, that these were normally successive layings by the same female. Combining all the years, two holes were used four

TABLE I. Breeding Season of *Chaetura brachyura*

	Number of nests started in half-monthly periods					
	1957	1958	1959	1960	1961	all years
April 1			1			1
2		1			1	2
May 1	5	4	1	3	1	14
2	4	3	2	3	2	14
June 1	1		4	3	4	12
2	1	1	5	1	2	10
July 1	3	2		1	3	9
2	1	4	2	1	1	9
Aug. 1	3		1	2	3	9
2					3	3
Sept. 1	1	1			1	3
Totals	19	16	16	14	21	86

times in a season, six holes three times, 22 holes twice, and 13 holes only once. These nests suffered a very high rate of predation, which undoubtedly raised the number of nesting attempts above what would be usual in a more successfully breeding population. If we consider only the nine cases where the first nesting attempt was successful, five were followed by a second laying and four were not. The breeding season is hardly long enough for three broods to be reared successfully.

Clutch-size

Chaetura species are known to have, for swifts, very large clutches, and the Short-tailed Swift is no exception. The mean number of eggs in 41 clutches was 3.6 (Table II). Mean clutch-size probably decreases in the course of the breeding season, since the only clutch of six eggs and all the clutches of five were laid in May.

TABLE II. Clutch-size of *Chaetura brachyura*

	Number of nests with clutch-size of					
	1	2	3	4	5	6
April 2				1		
May 1			2	2	2	1
2			3	3	2	
June 1		2	2	1		
2	1		2	1		
July 1			2	3		
2			2	2		
Aug. 1			3	2		
2						
Sept. 1			1	1		
All months	1	2	17	16	4	1

It was not possible to obtain exact data on the intervals between the laying of successive eggs, as my visits were not frequent enough, but incomplete data for ten nests showed that the normal interval is probably two or three days and longer intervals are not uncommon.

A clutch of nine eggs has been omitted from Table II, as it was certainly laid by more than one female. Apart from the abnormal size of the clutch, it could hardly have been laid by one bird as all nine eggs were laid within 14 days. It was of interest that the eggs were incubated successfully, though they were two or three deep in the nest; all nine hatched at about the same time. There was another instance in which the circumstantial evidence was strong that two females were laying in the same nest. Three eggs were laid between 0830 hours on June 1 and the afternoon of June 3, an abnormally quick rate of laying for a single bird. All three eggs were found broken below the nest on June 3, suggesting that the two birds were in conflict. For *Chaetura andrei,* Sick (1959) has reported a similar case of more than one female laying in the same nest. Such cases are presumably attributable to shortage of nest-holes.

Incubation and Fledging Periods

Because the colony was as a rule visited weekly, it was not possible to obtain incubation periods for most of the nests. But more frequent visits were made over limited periods, with the result that for three nests the incubation periods (from the laying of the last egg to the hatching of the last young) were found to be 17 ±1, 17-18 and 18 ±1 days. None of the less exact records was inconsistent with a 17-18 day incubation period.

Fledging periods were difficult to ascertain for the additional reason that the inspection of nest-holes near the fledging time was liable to cause the young to leave prematurely. Also it was found that the young birds return to their nest-hole by day after their first flight. Thus only very careful, repeated observations would show with certainty when undisturbed young first fly.

With these reservations, partial information was obtained on the fledging periods at eleven nests. At five of them, the young flew out on inspection at the ages of approximately 28, 29, 29, 32 and 34 days. One of those that flew when 29 days old was caught as it struggled to rise clear of the long savanna grass and was found to have a wing-length of 112 mm., 8 mm. shorter than the mean adult wing-length. At the six nests where there was no evidence of disturbance, the young left as follows:

(1) one of the two at 29-32 days, the other at 32-36 days.
(2) the first young at 32-36 days, the other two at 36-40 days.
(3) one of the two at 34-38 days, the other after 38 days.
(4) all four young before 35 days.
(5) both young at 35-42 days.
(6) the first two young before 36 days, the third after 36 days.

To sum up these observations, the young can fly if disturbed as early as 28 days after hatching; if undisturbed, they do not usually leave until they are 30-40 days old.

Like Chimney Swifts (*Chaetura pelagica*), young Short-tailed Swifts climb out of the nest while they are still unfeathered and cling to the wall near the nest. At one nest, one of the four nestlings was found clinging to the outside of the nest when 15 days old, the other three still being in the nest-cup. Two days later, at the age of 16-17 days, all four were clinging to the wall a few inches below the nest. At other nests the young were not recorded leaving the nest until three or four days later than this.

Intervals between Broods

The intervals between the ending of one nesting attempt and the laying of the first egg of the next clutch could not usually be ascertained exactly, but 27 intervals were known to within 4 days. These were as follows:

after successful fledging of previous brood: 4, 12, 13, 18, 24.

after loss of eggs: 9, 10, 10, 15, 17, 19, 24, 24, 27, 27, 31, 32, 32, 32, 35, 51, 74.

after loss of young: 17, 19, 29, 51.

Over half of the intervals are between 10 and 30 days. Some of the very long intervals may be false, due to the fact that an intervening clutch had been started and lost between my visits. Because of the variability of the intervals, the number of records is rather small for any certain conclusions, but there is a suggestion that relaying usually follows more quickly after the successful fledging of a brood than after a failure.

Nesting Success

This population of Short-tailed Swifts nesting in underground man-holes was singularly unsuccessful in its breeding; only 15 (17%) of the 86 recorded nestings resulted in fledged young. Usually eggs vanished soon after they were laid, but some losses occurred at all stages. However, hardly any information was obtained on the causes of failure. The possibility was not excluded that snakes and lizards could get into the holes and attack the nests, but there was no evidence that they did so. The only certain predator was a large spider (*Mygale* sp.). When I accidentally dropped two newly hatched nestlings on the floor of the hole, one of these spiders rushed out of a crevice, seized one of the nestlings before I could pick it up, and retreated back to its lair. The squeaks of the nestling ceased the moment it was seized and it appeared to be dead within a second. As this large spider can climb vertical walls it could be a regular predator of small nestlings.

Three nest-holes regularly filled with water after heavy rain, and several nests, as well as at least three adults, were lost in this way.

These observations can, however, have little significance in the ecology of the species as a whole. Underground man-holes must be such an unusual nest-site for the Short-tailed Swift that neither the high rate of nest failure nor the causes of failure are likely to be typical.

The Moult, and Roosting Habits

Two birds trapped on August 14, one caught on September 16, eight on September 18, and one on September 25 were all in various stages of moult. Only three other adults were caught, one in March and two in July, and none of these was moulting. Details of the sequence of moult are given in a later section.

At 1000 hours on September 16, 1957, a fine sunny day, one of the nest-holes which had not been in use for some weeks was found to contain about 50 adult swifts. On September 25, 50 birds were again found in this hole at 1020, and ten were found in another hole containing a nest with eggs, apparently deserted. The birds caught on these two days were in moult, as has been mentioned above. Subsequently it was found that during the moult the adults regularly spent part of the day in two or three of the holes, either clumped, as at night, or clinging scattered on the wall.

I visited the colony at night several times and found the swifts roosting in the holes all the year round, but in the months November-March their presence was irregular. Outside the breeding season, they tended to congregate in two or three holes, the same ones that they were found in by day during the moult, roosting in clumps of 30 or more birds together. As the breeding season approached their numbers declined, the roosting aggregations broke up, and each hole was finally occupied at night by a pair or three birds. As late as February, up to 50 birds were found roosting in the nine holes inspected; by early May the numbers had fallen to 21.

When disturbed at night, Short-tailed Swifts give the same wing-clattering display as has been described for the Chimney Swift (Fisher, 1958). The birds slowly raise their wings above the back, then spring away from the wall with a clattering sound, to land back in the same spot or a few inches away. The clattering appears to be made by the rapid clapping together of the wing-tips. Several birds in a clump will raise their wings together and clatter at the same time, so that the noise is quite startling to the intruder. There seems no doubt that it is an anti-predator display analogous to the hissing of tits and some other hole-nesting birds. After a few bursts of clattering a roosting clump becomes broken up, with the birds more evenly scattered over the sides of the hole.

Breeding, Moulting and Roosting of Other *Chaetura* Species

Extremely scanty information was obtained on the other *Chaetura* species. For Chapman's Swift nothing was found out except that the individual caught on November 27, 1960, was undergoing slight body moult.

For the Band-rumped Swift there were only two observations of note. On July 9 and 11, 1959, as already mentioned, a pair was found to be feeding young in a hole about 30 feet up in the trunk of a Chataigne tree (*Pachira insignis*). This is the first indication of the breeding site of the species. A flash photograph of Short-tailed Swifts roosting in one of the manholes on February 27, 1958, showed the presence among them of a single Band-rumped Swift. This appears to be the first record of roosting for the species.

More information came from the trapping program. Twenty-one Band-rumped Swifts were caught in mist-nets in the Arima Valley, 6 in January, 1 in February, 1 in April, 2 in August, 8 in October and 3 in November. One caught on August 3 was finishing its wing-moult, the two outer primaries not being full-grown. Another, caught on October 23, was probably just finishing its wing-moult as some of the primary coverts were growing but not the primaries themselves, which were fresh. These were the only examples of wing-moult. Eleven of the 17 birds trapped in the months October-January were undergoing body-moult. The weights of these trapped birds are given in the Appendix.

For the Gray-rumped Swift even less information was obtained from field observation. I once almost certainly saw a pair enter a cleft in an Immortelle tree (*Erythrina micropteryx*) about 1,000 feet above sea level in the Arima Valley at dusk, but the light was so bad that when the birds, which I had had under observation for half an hour as they circled the tree, finally entered, or appeared to enter, the hole, I could not be certain of what I had seen.

Forty-three Gray-rumped Swifts were caught in mist-nets, in several months of the year. An analysis of the moults of these birds is given in Table III. It will be seen that 9 of the 13 birds trapped between June 14 and November 6 were undergoing wing-moult, but none of the 29 birds trapped from January 5 to May 26. The bird trapped on May 26 had an incubation patch and weighed 16 gm., the highest weight recorded (see Appendix), and so was clearly laying eggs. This evidence suggests that the Gray-rumped Swift has much the same breeding season as the Short-tailed Swift.

Table III. Moult Data for Trapped *Chaetura cinereiventris*

	Number of individuals showing		
	Wing-moult	Body-moult only	No moult
Jan.		14	2
Feb.		2	
April		4	6
May			1
June	1		1
July			1
Aug.	1		
Oct.	3		
Nov.	4	2	

The Moulting Sequence in *Chaetura*

Nine moulting Short-tailed Swifts were examined, nine moulting Gray-rumped Swifts, and one moulting Band-rumped Swift. The wing-moult follows the pattern that is general in many birds; the primaries moult in sequence from inside outwards and the secondaries centripetally from the two ends. For the primary moult, which spans practically the entire period of the moult, the following stages are recognized, using a method of notation adapted from Miller (1961): Stage 1, 1st (innermost) primary growing, 2-10 old; Stage 2, 2nd primary growing, 3-10 old; and so on to Stage 9, 9th primary growing, 10th old; Stage 10, 10th primary growing.

The secondaries are much shorter than the primaries and their replacement is much more rapid. They do not begin to be moulted until the primary moult is well advanced, and they finish before the primaries finish. No difference was noted between the Short-tailed and Gray-rumped Swifts in this respect. Three birds were examined whose primary moult was at Stage 6;

all had old secondaries. Two were examined at Stage 7; in one the secondaries had begun to moult, but not in the other. Three at Stage 8 were all replacing their secondaries. Two at Stage 9 and two at Stage 10 had all finished replacing them.

The tail moults centripetally. It begins after the primary moult has begun and ends at about the time that the primary moult ends. In the Short-tailed Swift it seems, by extrapolation from the specimens examined, that the tail begins to moult at Stage 4 or 5 in the primary moult, but no birds were examined at these stages. In the Gray-rumped Swift the tail moult begins later, at Stage 7 or 8. This difference between the two species is apparent from the following comparison of birds at the same stages of primary moult:

	Short-tailed Swift	Gray-rumped Swift
Stage 6.	Two birds, both half way through tail-moult	One bird, tail not moulting
Stage 7.	Two birds, about three-quarters through tail-moult	—
Stage 8.	One bird; tail-moult nearly complete	Two birds; one just starting tail-moult, the other half way through
Stage 9.	One bird; tail-moult complete	One bird; tail-moult nearly complete
Stage 10.	—	Two birds; tail-moult nearly complete

Besides being less regular in its sequence than the wing-moult, the tail-moult is also sometimes not complete Two birds that were not moulting showed incomplete replacement of the tail-feathers: in one the outermost pair of feathers, and in the other the central pair, were old and worn, the rest of the tail-feathers being new.

The Breeding of *Cypseloides rutilus*

Belcher & Smooker give records of three clutches, from two nests, and Orton (1871) mentions the nest-site. These appear to be the only breeding records published for the Chestnut-collared Swift. During the present study ten occupied nests were found, and two other unoccupied nests. Nests are usually repaired and used year after year, and the ten occupied nests gave records of 33 nestings.

Nest and Nest-site

The nest is a substantial bracket, semicircular in horizontal section, with a shallow depression for the eggs. It is made of various plant fibres, usually including some moss, and is fixed, presumably with saliva, onto a smooth rock-face or wall, a few feet above water. The natural nest-sites in the Northern Range of Trinidad are vertical or overhanging rock-faces at the sides of mountain streams or gorges; eight nests were found in such sites. In addition, one nest was found under a bridge, about 16 feet above the water, and two were found in culverts, through which small streams flow under the main road that runs up the Arima Valley.

The remaining nest was in a small sea cave on the north coast. Owing to the collapse of its roof, this cave had become a hole with a low tunnel leading through to the sea. The nest was situated 7 feet up, under an overhang above the landward end of the tunnel. Chestnut-collared Swifts were also seen during the breeding season entering and leaving La Vache cave on the north coast, a large sea cave occupied by Oilbirds (*Steatornis caripensis*), and flying out of a sea cave on the north side of Huevos Island, off the northwest corner of Trinidad. There are many caves along the north coast of Trinidad and the off-lying islands, and doubtless Chestnut-collared Swifts breed in them in considerable numbers.

Breeding Season and Breeding Statistics

The breeding season is much the same as that of the Short-tailed Swift; the first eggs were laid in April or May in each year, and the last in August. The date of laying of 32 clutches is shown in Table IV (one nest could not be dated accurately enough for inclusion). Is is curious that two of Belcher & Smooker's three clutches fall outside these limits. One of them was accurately dated August 31-September 2, only a little later than the latest of my nests; the other was found on November 10. The possibility that the

TABLE IV. Breeding Season of *Cypseloides rutilus*

	Number of nests started in half monthly periods
April 2	1
May 1	3
May 2	3
June 1	4
June 2	4
July 1	2
July 2	6
Aug. 1	5
Aug. 2	4

latter was an old deserted clutch is not mentioned.

In all cases except one, the clutch was two eggs. The interval between the laying of the two eggs was not accurately determined, but at one nest it was at least two days and the other records are all consistent with a two-day interval between eggs.

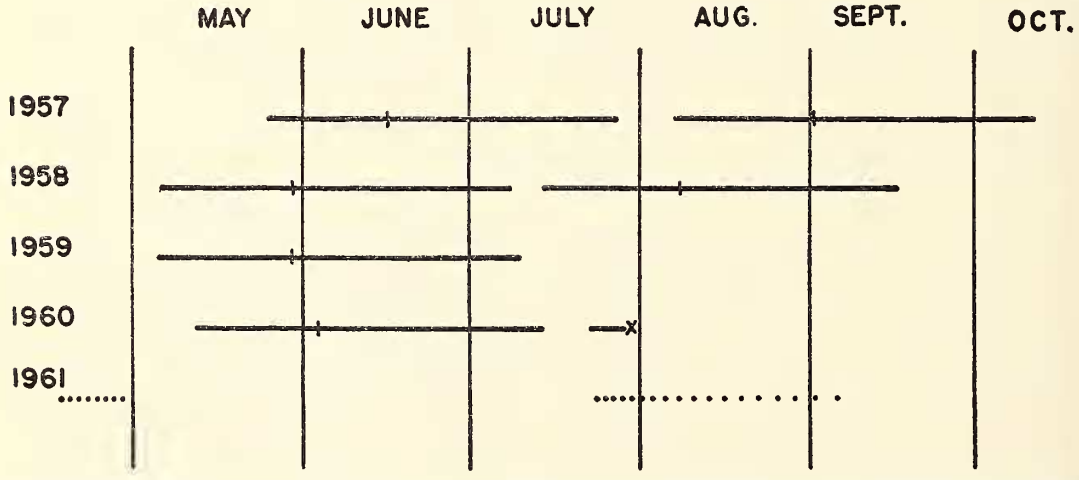
The single clutch of one egg was laid in circumstances that suggested a bird breeding for the first time. The nest was begun in June, 1961, in a site that was known not to have been used for at least four years, as the place had been under fairly frequent observation. Building was slow and was hindered by heavy rain which caused part of the nest to fall away. The nest was finally completed by the third week of August and the single egg was laid a few days later.

The incubation period (from the laying of the second egg to the hatching of the second young) was ascertained at three nests to be 22, 22-23 and 24 days. Fledging periods were ascertained to within a few days at four nests, and were found to be 37-44, 38-40, 39-40 and 39-41 days. At another nest the date of hatching was not known, but the period from the laying of the second egg to the flying of the two young was found to be 60-63 days.

Two of the nests that were followed through a complete breeding season were used only once, ten were used twice and one was used three times, the first two attempts being unsuccessful and the third successful. The season would not be long enough for three broods to be reared.

The most complete record was obtained for one nest-site that was occupied for five successive years, though eggs were not laid in it in the fifth year. Two broods were reared in 1957, two in 1958 and one in 1959. In 1960 the first brood was reared and a second clutch was laid but was lost soon afterwards. In the off-season 1960/61 the nest, which was only about four feet above the water of a rock-bound pool in a mountain stream, was washed away. Another nest was built in April, 1961, a few feet away, but even nearer the water; it remained empty for several weeks, then it too was washed away in July. The bird returned to the old site and built a new nest in late July and August; but probably by then the season was too far advanced and no eggs were laid in it. The history of this nest-site in shown graphically in Text-fig 1.

Intervals between broods (from the flying of the young to the laying of the first egg of the next clutch) were rather short. Those that were known to within a range of six days were as follows: 4-8, 5-11, 6-11, 9-11, 10-13 days. In



TEXT-FIG. 1. Occupation of a Chestnut-collared Swift nest-site over five breeding seasons. Each nesting is indicated by a heavy line, and the hatching date by a short bar. Dots: nest-building. For further details see text.

addition there was one instance of the first egg of the second clutch being laid 3-5 days before the single nestling of the previous brood left the nest. The two intervals following loss of eggs were longer than those following successful fledging: 13-17 and 21-23 days.

Chestnut-collared Swifts' nests seem to be safe from predators, and breeding success was fairly high: 15 (63%) of the 24 nestings which could be used for analysis resulted in fledged young. Two clutches were soaked by water running down the rock-face after heavy rain and were abandoned. The eggs or young disappeared from six nests, and one was deserted for no known reason. Although the hatching rate was high in the successful nests (27 out of the 29 eggs that survived to the expected date of hatching), there were a few losses of eggs during incubation, and some losses of young at all stages, and the mean number of young leaving 18 successful nests (all of which had clutches of 2 eggs) was 1.3.

An estimation of the reproductive rate can be made from these figures, which there is no reason to think are untypical. If the mean number of nesting attempts per year is taken to be two, nesting success is 63%, and the number of young fledging from successful nests is on average 1.3, each breeding pair will rear on average 1.6 young per year.

Adaptations to Cliff-nesting

There is suggestive evidence that birds which nest in safe sites tend to have longer incubation and fledging periods than related species nesting in sites more exposed to predation, presumably because the selective pressure for quick development is relaxed (Lack, 1954). This may be part of the reason for the long incubation and fledging periods of the Chestnut-collared Swift compared with *Chaetura* species, which are almost certainly tree-hole nesters by origin.

If clutch-size is limited by the number of young that can be fed, a reduction in the rate of development of the young will enable clutch-size to be increased. As Lack points out, there is good evidence that this has happened: passerines with safe nest-sites tend to have not only slower rates of development but also larger clutches than passerines with exposed nest-sites. The small clutch of the Chestnut-collared Swift and of other *Cypseloides* species (Lack, 1956), compared with *Chaetura* species, is contrary to this rule. Probably it is due to the nature of the nest-site. *Chaetura* nestlings climb out of the nest when half-grown, so that large families can be reared from their small nests, but it would be impossible for half-grown Chestnut-collared Swifts to cling safely to the smooth, often overhanging rock-faces to which the nest is fixed, and two full-grown young are as many as can be accommodated on the flattish top of the nest. Towards the end of their nestling period they exercise their wings while hanging to the outer rim of the nest, a method also recorded for the Black Swift (Bent, 1940).

An alternative explanation for the small clutch-size in *Cypseloides* is that their method of feeding is such that they are unable to find food for more than one or two nestlings. As mentioned above, Chestnut-collared Swifts feed higher than the *Chaetura* species, and the density of flying insects must in general decrease with altitude. The point cannot be ruled out, yet it seems unlikely that in many different habitats, and over a wide range of latitude, *Chaetura* species are always about three times as efficient at collecting food as *Cypseloides* species.

Lack (1956) has stated that among swifts only the Hemiprocninae and *Cypsiurus* develop nestling down, presumably for warmth and camouflage, as they nest in exposed sites. But downy young have been recorded for the Black Swift (Bent, 1940), and in the Chestnut-collared Swift, too, the nestling develops thick down. Like the Black Swift, the Chestnut-collared Swift is hatched naked and grows its down after a few days; Table V gives details of the development of a nestling whose exact age was known. Presumably in *Cypseloides* the nestling down is primarily an adaptation for heat conservation. The shady and damp places where they nest are several degrees colder than the surroundings.

Hovering Flight in *Cypseloides* and *Chaetura*

It does not seem to have been recorded that some swifts on occasion adopt a hovering method of flight in which the wing action must be more like that of a hummingbird than of a swift in normal flight. During night visits to the Oilbird colony in the Arima gorge, roosting Chestnut-collared Swifts were sometimes disturbed by my torchlight and would fly slowly about the cave with a hovering flight, the body being rather upright, until they came in contact with a rock-face to which they could cling. Twice I easily caught a bird as it hovered slowly towards me and clung to my clothing. In the same gorge in the day-time Chestnut-collared Swifts, when disturbed from their nests, would fly off with the usual rapid flight, as do those disturbed from nests in more open places along streams. Limited observations suggested that they normally also fly to their nests with rapid flight. Under undisturbed conditions, the hovering flight is probably used by the swifts when going to roost in caves and dark gullies at dusk.

TABLE V. Development of Nestling Chestnut-collared Swift

Date	Age	Description
3 June	Just hatched	Naked; skin pink; down rudiments visible as dark spots on upper surface.
6 June	3 days	Down visible as blackish streaks, not yet through skin.
9 June	6 days	Down beginning to sprout on upper surface. Rhythmic clutching movements with feet when removed from nest.
13 June	10 days	Eyes just open; gray woolly down all over upper surface, much sparser on underside.
17 June	14 days	Thick down above and below. Primary and secondary coverts up to 1 mm. out of sheath; primaries and secondaries as long pin-feathers.
22 June	19 days	Thick down all over body; feathers in sheath beneath down; front half of head feathered, feathers of fore-crown sooty with rusty fringes; wing-feathers 10-15 mm., tail-feathers c. 5 mm. beyond sheaths.
27 June	24 days	Head well feathered; wing- and tail-feathers well grown.
8 July	35 days	Nearly ready to fly; collar dull rufous.
11 July	38 days	Still in nest in late afternoon.
14 July	41 days	Nest empty.

and perhaps going to nests in clefts where a straight run-in is not possible. Its value in allowing safe flight in dark and confined places is obvious.

Short-tailed Swifts were seen to use the same hovering flight when rising vertically out of the man-holes where they nested. As they rose clear of the hole they at once changed to the usual rapid flight and flew off low, skimming the grass. *Chaetura* species must always fly thus when they leave narrow chimneys or other cavities with a top hole.

SUMMARY

The breeding and other aspects of the biology of swifts of the genera *Chaetura* and *Cypseloides* were studied in Trinidad, West Indies. The status of the five resident and one migrant species is summarized.

A small breeding colony of *Chaetura brachyura* was kept under observation for five breeding seasons. The breeding season extended from April to early September. Most birds made from one to three nesting attempts in each season. Mean clutch-size was 3.6 eggs, the incubation period was 17-18 days, the fledging period 30-40 days. Breeding success was low, but was considered not to be typical, owing to the unusual nest-sites (underground sewer manholes). After the breeding season, moulting birds often spend part of the day clumped together in the nest-holes.

Data are presented on weights and measurements of *Chaetura brachyura, C. cinereiventris* and *C. spinicauda,* and on the sequence of moult in *C. brachyura* and *C. cinereiventris.*

Data are given on 33 nestings of *Cypseloides rutilus,* nesting on overhanging cliffs above streams, under bridges and culverts, and in sea caves. The species is single or double brooded, and repairs and re-uses its old nests year after year. The clutch normally consists of 2 eggs. Incubation lasts 22-24 days, and the fledging period is about 40 days. The young is hatched naked, but develops a thick covering of down. The small clutch, the long development period and the nestling down are all considered to be correlated with the specialized nest-site.

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Appendix

Wing-Lengths and Weights

The figures in parentheses give the number measured, and are followed by the range and the mean.

Weights were recorded immediately after capture, except where specified. Wings were measured in the normally closed position, the primaries retaining their natural curvature.

Chaetura brachyura

Wing (10) 116-130, 119.9 mm.
Weight (11) 17-30, 19.8 gm.

The large weight-range is due to a single bird of 30 gm.; all the others were between 17 and 22 gm. This very heavy bird, a female, was caught on March 22, about six weeks before breeding began; it was very fat, the ovary being still quite small. The other birds were all caught in August and September.

Chaetura cinereiventris

Wing (37) 98-105, 101. 5 mm.
Weight (43) 12.5-16, 13.8 gm.

Chaetura spinicauda

Wing (19) 98-107, 102.6 mm.
Weight (21) 13-18, 14.2 gm.

Chaetura chapmani

Wing (1) 120 mm.
Weight (1) 25.5 gm.

Cypseloides rutilus

Weight (2) 20, 22 gm.

The lighter of the two birds was captured in the evening and weighed early next morning.

Cypseloides zonaris

Weight (3) 60, 63.5, 74 gm.

The two lighter birds had been knocked down with sling-shots from a low-flying flock and had been several hours without food when weighed.